

47. On Variation in the Medusa of *Mærisia lyonsi*. By CHARLES L. BOULENGER, M.A., F.Z.S., Lecturer on Zoology in the University of Birmingham.

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(Plate LIX.* & Text-figures 222-228.)

In 1908 I published an account [1]† of a new lacustrine Hydromedusan, *Mærisia lyonsi*, obtained by Dr. Cunningham and myself from the brackish waters of Lake Qurun in the Fayûm Province of Egypt.

In my paper, whilst describing the anatomy of this interesting form, I called attention to the fact that the number of tentacles and radial canals in the medusa stage was subject to much variation, and mentioned that in a series of 400 individuals which I examined, 55, or nearly 14 per cent., differed from the normal.

My description of the abnormal specimens was very short, and it has been suggested to me that it would be of interest to furnish a more detailed account of the variation of this medusa, as well as to figure some of the more peculiar abnormalities. This I was all the more prepared to do, as further study of the collection had revealed additional points of interest in connection with this phenomenon.

Variation is known to occur frequently in jelly-fishes‡, and in some species it has been very carefully studied; although in many cases the series dealt with were numerically far greater than the one at my disposal, I know of no form in which such a variety of abnormalities occur as in *Mærisia*. The interest of the series I am about to describe is not diminished by the fact that all its members were collected in one locality and belong to the same sex.

As the greater part of my material had already been distributed when I decided to take up this subject again, it was necessary to re-examine the specimens in the Natural History Museum, London, and in the Cambridge Museum of Zoology; for permission to do this, I have to thank Mr. R. Kirkpatrick and Mr. L. Doncaster, under whose charge the specimens are preserved in these institutions.

In my description of *Mærisia lyonsi*, I drew up the following table to show the number and arrangement of the radial canals

* For explanation of the Plate see p. 1056.

† The figures in brackets refer to the List of References on p. 1055.

‡ Cf. List of References on p. 1055.

and tentacles in 400 medusæ taken at random from the material at my disposal:—

Table showing the Number and Arrangement of the Radial Canals and Tentacles in 400 individuals.

Number of Individuals.	Number of Radial Canals.	Number of Tentacles.				
		Perradial.	Interradial.	Adradial.	Subradial.	Total.
1	3	3	—	—	—	3
345	4	4	—	—	—	4
1	4	4	1	—	—	5
1	4	4	1	2	—	7
1	4	4	—	1	—	5
2	4	4	2	4	—	10
10	4	4	4	—	—	8
28	4	4	4	8	—	16
1	4	4	4	8	6	22
9	5	5	—	—	—	5
1	6	6	—	—	—	6
Total 400						

It will be noticed that the 55 abnormal individuals fall naturally into two well-marked groups:—(a) which includes those medusæ which deviate from the normal tetramerous symmetry; and (b), which includes medusæ with the normal number of radial canals and primary, perradial tentacles, but possessing, in addition, secondary tentacles situated between the four primary ones and not connected with the stomach by means of radial canals.

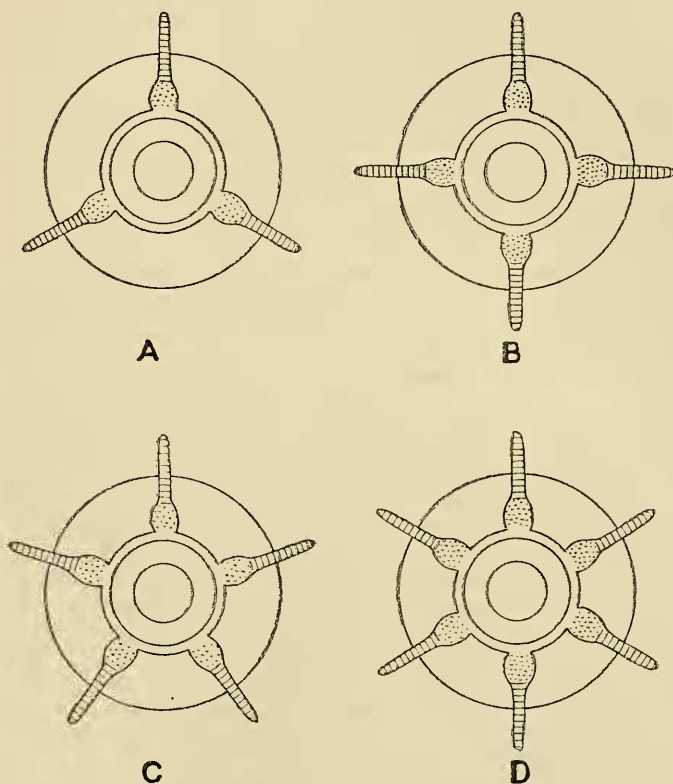
It is my intention to discuss these two groups separately, as it is obvious that in them we are dealing with two completely distinct phenomena.

(a) The normal medusa of *Mærisia lyonsi* is provided with four radial canals at the distal extremities of which the four perradial tentacles are given off. The gonad-bearing region of the stomach is produced into four perradially situated pouches which in the adults extend as finger-shaped diverticula for a considerable distance along the radial canals.

Eleven specimens out of the 400 medusæ examined (*i. e.* 2·75 per cent.) were found to deviate from this general tetramerous symmetry; one medusa possessed only three radial canals, three tentacles and three gonadial diverticula; nine medusæ had five, and one had six of these structures. This type of variation is known to occur in many species of medusæ which are normally tetramerous in symmetry; among craspedote forms it has been studied best in *Obelia* (*Eucope*) [2], *Clytia* [3], *Sarsia* [4, 5], *Rathkea* (*Lizzia*) [7], *Podocoryne* [8], *Gonionemus* [8], and *Limnocyda* [9].

Limnocrida being another African lacustrine form is of particular interest. Günther found that out of 70 individuals collected by Dr. Cunningham in Lake Tanganyika, 54 medusæ showed the typical number (four) of radial canals, whilst 16, or 24 per cent., had five or more; as in the case of *Mærisia*, specimens with five radial canals were commoner than those with a larger number. Günther, however, found no medusæ with only three canals, but such trimerous forms have been described in other genera, e. g. *Podocoryne* [8] and *Rathkea* [7].

Text-fig. 222.

*Mærisia lyonsi*.

Diagrams to show the arrangement of the tentacles in four medusæ.

B represents the normal tetramerous form.

Similar variations occur in several members of the Scyphomedusæ: perhaps the most complete account of the phenomenon is that given by E. T. Browne for *Aurelia aurita* [11, 12]. This author examined the variation in the number of tentaculocysts in the ephyra larvæ and adults of the jelly-fish, and found that

20.9% and 22%, respectively, were abnormal, the number of these sense-organs ranging between 6 and 15, the normal number being, of course, 8. These figures, however, include a number of specimens which are undoubtedly teratological monstrosities.

Browne pointed out that variation in the number of tentaculocysts does not necessarily interfere with the other organs of the body, but that there is a correlated variation between the number of genital pouches and buccal arms as shewn by eight specimens:—4 individuals had 3 genital pouches and 3 buccal arms, 1 had 5 pouches and 5 arms, and 3 had 6 of these organs.

In *Morisia* there must necessarily be a correlation between the number of primary tentacles and radial canals, since recent researches on the development of the gonophores of Hydromedusæ [13, 14] have shown that these structures arise together from the endodermal pouches of the young medusa-bud.

There is also a correlated variation between the number of radial canals and gonadial pouches, and this is only what we should expect as the latter structures spread outwards from the stomach on to the radial canals. The single 6-rayed specimen, however, had one gonadial pouch very poorly developed although the other five were quite normal.

It is interesting to note that variation in the number of primary radii in the medusa does not necessarily affect the symmetry of the manubrium; this point is well shown in the sections figured on Pl. LIX.

A normal medusa with four tentacles, radial canals and gonadial diverticula has the distal part of the manubrium provided with a similar number of conspicuous endodermal ridges or tæniolæ, which can be seen in the section figured (Pl. LIX. fig. 1); a similar section through a pentamerous individual (Pl. LIX. fig. 2) demonstrates the fact that, although five canals and gonads are well developed and the manubrium appears almost pentagonal, the number of endodermal ridges is not affected, although their symmetrical arrangement is disturbed.

The above is in accordance with the observations of other investigators:—Agassiz and Woodworth [2] examined 4000 specimens of *Obelia* (*Eucope*), but noted no variations in the shape of the digestive cavity or in the number of the actinal lobes of the manubrium, even in specimens with five or six radial canals in place of the normal number (four) the actinal lobes being always found to be four in number.

A. G. Mayer [3] has also made some interesting observations which bear on this point. This author has made a careful study of the medusa *Pseudoclytia pentata*, the only Leptomedusan which is normally pentamerous, and which he considers to be derived from some species of *Clytia* (*Epenthis*), e.g. *C. folleata*. In *Pseudoclytia pentata* there is much variation both in the number of radial canals and in the number of oral lips; but whilst the former incline towards the production of more than five canals, the oral lips show a decided tendency to revert to the ancestral condition of four.

As mentioned before, variation in the number of radii is of common occurrence in medusæ, and in the above-described varieties of *Marisia lyonsi* we are undoubtedly dealing with a quite ordinary case of meristic variation. As Bateson remarks in his well-known book on the Study of Variation [15]:—"In radial series phenomena analogous to those of the variation in linear series are seen in their simplest form. Just as in linear series the number of members may be changed by a reconstitution of the whole series so that it is impossible to point to any one member as the one lost or added, so may it be in the meristic variation of radial series: and again as in linear series, single members of the series may divide. Between these there is no clear line of distinction."

In the abnormal specimens of *Marisia*, I do not think that we are dealing with cases of division or suppression of one or more radii; from what we now know of the development of medusa-buds [13, 14], it seems that the variation is in the number of radial pouches formed in the early bud.

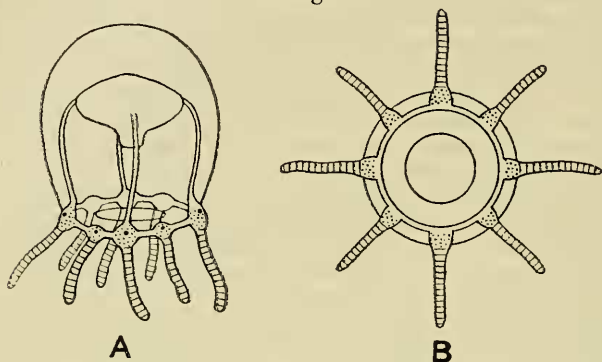
Since each pouch develops the radial canal and perradial tentacle of its own section of the medusa-bell, such variation explains the correlation of the numbers of these two sets of organs. The fact that the manubrium is independent of the organs situated in the umbrella is a point decidedly in favour of this view. I have, unfortunately, not been able to study the development of an abnormal specimen, all the medusa-buds I have sectioned proved to be of normal tetramerous symmetry.

(b) The second group of abnormal individuals includes a number of tetramerous medusæ which bear secondary tentacles between the four primary perradial ones. These secondary tentacles may be interradii, adradial or subradial in position, and differ from the perradial ones in not communicating with the gastric cavity by means of radial canals; they are developed from the ectodermal and endodermal cells of the umbrella-margin, their cavities being in communication with the circular canal.

Altogether 44 of the 400 tabulated individuals exhibited this kind of abnormality, which is of a very peculiar type; I have not been able to find any record of a similar case in a medusa which normally bears primary tentacles only. There are, of course, numerous tetramerous medusæ which normally possess such secondary tentacles (e. g., *Podocoryne*, *Territopsis*, *Oceania*, *Limnocoïda*), and they are known to start life with the four primary ones only, the secondary tentacles being developed as the animals grow, usually in some definite sequence. Thus, in the majority of cases, the second set of tentacles to appear is the interradii one, four of these structures growing simultaneously from the umbrella-margin between the four perradial tentacles. Eight adradial tentacles are formed next, two in each quadrant occupying the interspaces between the interradii and perradial ones, and their formation may be followed by the appearance of a varying number of subradial tentacles.

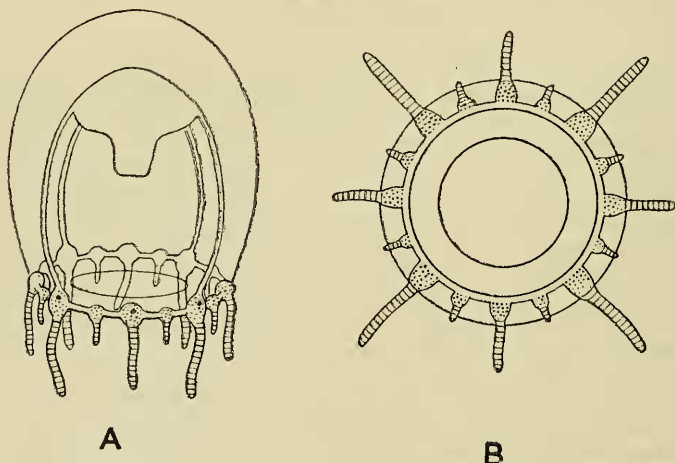
In such medusæ it is obvious that the number of secondary tentacles is correlated with the size of the individuals, the older and larger medusæ possessing a greater number of these structures than the smaller and younger ones. In *Maerisia* we are certainly

Text-fig. 223.



Medusa bearing four interradial tentacles in addition to the four perradial ones at the extremities of the radial canals. In this and in the three following text-figures A represents the medusa as seen in a side view, B its oral aspect.

Text-fig. 224.



Medusa with four interradial and eight adradial tentacles in addition to the four primary ones.

not dealing with a phenomenon of this kind, for the larger and more mature medusæ are, with rare exceptions, unprovided with secondary tentacles. In order to show this point more clearly, I divided the 400 individuals which I examined into two

groups:—(i.) including medusæ with an umbrella-diameter measuring between $\frac{1}{2}$ and 2 mm., and (ii.) with a diameter measuring from $2\frac{1}{2}$ mm upwards.

Group (i.) contained 278 individuals of which 39, or about 14 %, possessed supernumerary tentacles between the four primary ones, whereas of the 122 larger medusæ belonging to group (ii.) only 5 were provided with such structures.

Sexual dimorphism is known to occur in a few species of medusæ,* but I have assured myself that this is not the case with the specimens I am describing; microscopic examination, by means of sections and whole mounts, showed that all the medusæ of *Marisia* in my collection belonged to the male sex, whether bearing secondary tentacles or not.

It must be obvious from the above account that the kind of variation I have just described is of a nature totally different from that treated of in the first section of this note. We are certainly not dealing with a case of ordinary meristic variation, and the only conclusion I can arrive at is that these multitentacular medusæ form a distinct variety which has arisen as a mutation from the normal form: it will be interesting to discover whether this variety will maintain itself in Lake Qurun.

Altogether, forty-six † multitentacular specimens have been examined by me; it was found that the number of secondary tentacles varied considerably. 10 individuals possessed four interradial tentacles as well as the four primary perradial ones (text-fig. 223); 28 had twelve secondary tentacles, four interradial and eight adradial (text-fig. 224); and 3 possessed subradial tentacles in addition to these, the medusa illustrated in text-fig. 225 (p. 1052) having as many as eight of these structures, two in each quadrant, situated between the interradial and adradial tentacles.

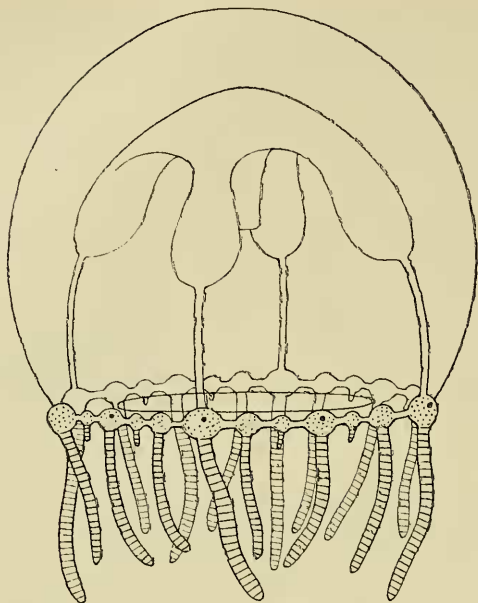
The sketches referred to above, although considerably enlarged, are drawn to scale; they exhibit the fact that this variety of *Marisia lyonsi* follows the general rule for multitentacular medusæ, in that the number of secondary tentacles increases with the size and age of the individuals. The sequence of the development of the secondary tentacles is also quite normal in the specimens just described.

Although the majority of the multitentacular specimens of *Marisia* exhibited a perfect radial symmetry and developed their secondary tentacles in a perfectly normal order, a few medusæ proved abnormal in this respect and showed marked asymmetry. One specimen had a single interradial tentacle developed between two perradial ones, whilst another bore interradial and adradial tentacles also in a single quadrant only. Again, two medusæ had these organs developed in two of the quadrants (text-fig. 226), and a third had secondary tentacles in

* E. g. *Stomatoca dinema* Agassiz, and *Orechistoma pileus* Lesson: see Mayer (10) pp. 111 and 219.

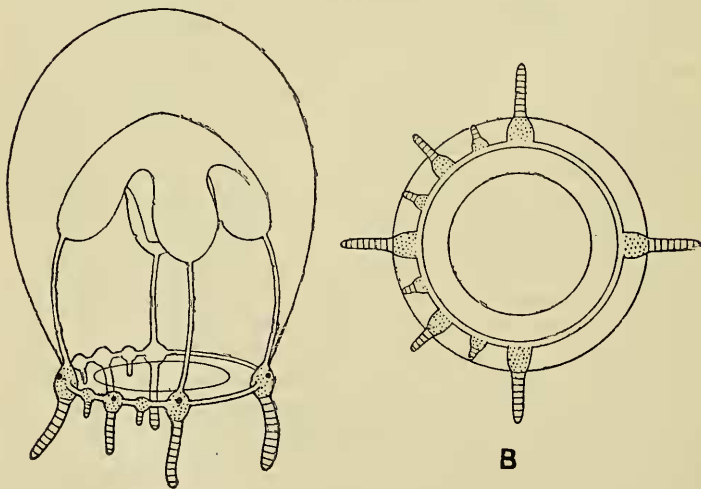
† Two of these specimens were not included in the Table on p. 1049.

Text-fig. 225.



Multitentacular medusa with twenty secondary tentacles.

Text-fig. 226.

**A****B**

Asymmetrical medusa bearing secondary tentacles in two quadrants only.

three quadrants. This specimen had interradiar, adradial and subradial tentacles in two of these, whilst the third quadrant carried only a single adradial one*.

Günther has shown that in *Limnocoñida* [9], tentacles of a particular order are often fully formed in one quadrant before there is any trace of them in the others. Browne also has called attention to the fact that in *Podocoryne carnea* [7] the young medusæ do not always leave the hydroid colony with the same number of tentacles, all have four perradiar ones but the number of interradiar tentacles varies, some having two or three instead of four, and one specimen he noticed to have a single one only.

I do not think that in the case of the asymmetrical medusæ of *Mærisia* to which I have just referred, we are dealing with any retardation in the development of the tentacles in certain quadrants; some of these individuals were of considerable size and the gonadial diverticula well developed (*cf.* text-fig. 226), yet certain quadrants showed no signs whatsoever of secondary tentacles, although other quadrants possessed tentacles of the third or even fourth order.

These five asymmetrical medusæ clearly indicate that each quadrant is capable of forming secondary tentacles quite independently of the other quadrants of the bell. That this can occur in a radially symmetrical animal is distinctly stated by Bateson [15] who remarks, that in radial series "as in Linear Series, Variation, whether Meristic or Substantive, may take place either in single segments (quadrants, sixths, etc.), or simultaneously in all the segments of the body." This statement was based on observations made on two medusæ, *Clavatella* (*Eleutheria*) *prolifera* and *Aurelia aurita*.

Clavatella is a medusa which normally bears a single ocellus at the base of each of its six tentacles. Claparède [16] has called attention to the fact that these ocelli are sometimes doubled; this duplicity may occur at the base of a single tentacle or occasionally at the base of each tentacle instead of one.

Bateson also quotes the observations made by Romanes [4, 5] on *Aurelia aurita*. In this form, in addition to changes symmetrically carried out in the whole disc, one or more quadrants may vary independently. Thus one specimen is figured in which two quadrants are normal (*i.e.*, each possesses one generative organ and a set of radial canals) but the other half-disc is divided into three. Similarly a particular quadrant may possess two sets of organs or even three, the other three quadrants being normal or nearly so.

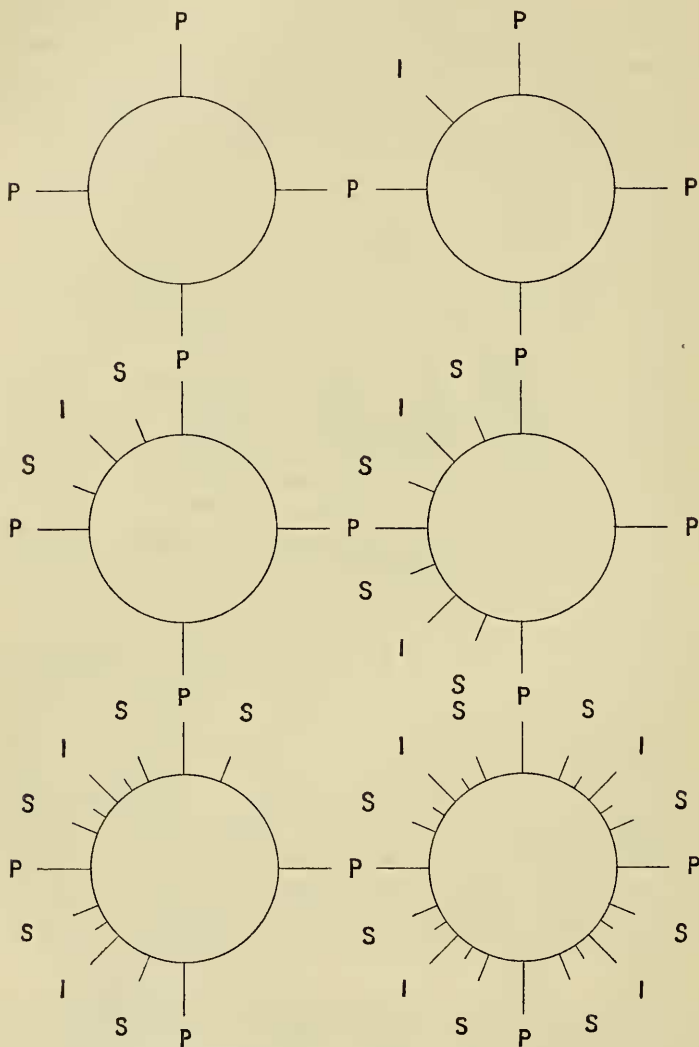
In addition to the forms described above, three other medusæ showed abnormalities of a quite different type, which, although known to occur in other genera, I consider worth recording.

In the first of these specimens, which was normal as regards

* This specimen is one of those not included in the Table published in my original paper on *Mærisia lyonsi*.

the number of its tentacles, one of the latter organs was branched in such a way as to present the appearance of a smaller tentacle growing out laterally from a perradial one.

Text-fig. 227.



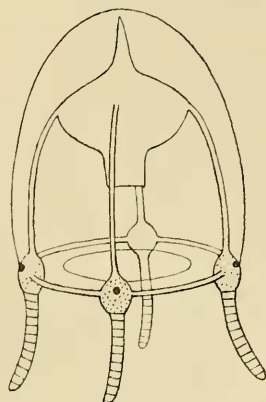
Diagrams showing the arrangement of tentacles in a normal and five abnormal medusae of *Maurisia lyonsi*.

P. Perradial tentacle. I. Interradial tentacle. S. Secondary tentacle in an adradial position. The subradial tentacles are not lettered.

Such branched or bifurcated tentacles have been recorded previously by several authors, among whom Agassiz and Woodworth [2] have described the phenomenon in medusæ of *Obelia* (*Eucope*), and Hargitt [8] came across a similarly abnormal specimen of *Gonionemus*.

It seems highly probable that such abnormalities are not congenital, these bifurcated tentacles having no doubt arisen as the result of injury to normal ones.

Text-fig. 228.



Abnormal medusa in which the apical canal is retained.

The abnormality presented by the other two medusæ is of greater systematic interest: each of these specimens possesses a well-developed apical canal which projects from the base of the stomach into the jelly at the summit of the umbrella (text-fig. 228). This peculiarity is obviously due to the fact that these specimens have retained the greater part of the canal which in early life connected the cavity of the medusa-bud with that of the parent-hydr oid.

The presence of an apical canal was at one time considered to be a specific character of some importance, but recent systematists* have shown that such a canal occurs frequently as an individual variation in many species which normally lose this organ in the adult stage.

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* Cf. Mayer's remarks on *Sarsia prolifera*, and other species of this genus (10).

† This list includes only those memoirs actually referred to in the text of this paper; for a more complete bibliography I must refer the reader to Dr. Mayer's recently published monograph (10).

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EXPLANATION OF PLATE LIX.

Fig. 1. A transverse section through a normal adult medusa of *Mærisia lyonsi*. The section shows the four radial canals and gonadal diverticula, as well as the four endodermal ridges in the manubrium.
end., endodermal ridge. *g.p.*, gonadal diverticulum. *lam.*, endodermal lamella. *man.*, manubrium. *r.c.*, radial canal.

Fig. 2. A similar section through a pentamerous specimen of the same species. Note that although five radial canals and gonadal diverticula are well developed, only four endodermal ridges occur in the manubrium. Cf. p. 1048.

Lettering as in fig. 1.